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Circularly polarized light as a communication signal in mantis shrimps

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Summary

Animals that communicate using conspicuous body patterns face a trade-off between desired detection by intended receivers, and undesired detection from eavesdropping predators, prey, rivals, or parasites [1–10]. In some cases, this trade-off favours the evolution of signals that are both hidden from predators and visible to conspecifics. Animals may produce covert signals using a property of light that is invisible to those that they wish to evade, allowing them to 'hide in plain sight' (e.g. dragonfish can see their own, otherwise rare, red bioluminescence [11–13]). The use of the polarization of light is a good example of a potentially covert communication channel, as very few vertebrates are known to use polarization for object-based vision [14, 15]. However, even these patterns are vulnerable to eavesdroppers, as sensitivity to the linearly polarized component of light is widespread among invertebrates due to their intrinsically polarization sensitive photoreceptors [14, 16]. Stomatopod crustaceans appear to have gone one step further in this arms-race, and have evolved a sensitivity to the circular polarization of light, along with body patterns producing it [17]. However, to date we have no direct evidence that

any of these marine crustaceans use this modality to communicate with conspecifics. We therefore investigated circular polarization vision of the mantis shrimp *Gonodactylaceus falcatus* [18] and demonstrate that 1) the species produces strongly circularly polarized body patterns; 2) they discriminate the circular polarization of light; and 3) that they use circular polarization information to avoid occupied burrows when seeking a refuge.

Keywords: Circular polarization, signalling, stomatopod, visual ecology, *Gonodactylaceus falcatus*

Results and Discussion

Circular polarization body patterns

We found that *Gonodactylaceus falcatus* displays distinct polarization patterns (Figure 1). Photopolarimetry reveals a relatively low degree of linear (< 0.1) or left-hand circular polarization (> -0.1) across many body areas, but with highly left-hand circular polarized signals (from -0.4 to -0.47; n=4) on legs and uropods (tail). One individual had a maximum left-hand circular polarization of -0.59 and -0.45 reflecting from the legs and uropods respectively. We found no right-hand circular polarization patterns on *G. falcatus*. In contrast to Chiou et al's. (2008) observations in *Odontodactylus cultrifer*, we found no striking evidence of sexual dimorphism in circular polarization (CP) patterns in *G. falcatus*. It is possible that *O. cultrifer* uses CP to silently communicate gender information to other conspecifics, while the role of the CP patterns in *G. falcatus* is different (e.g. for species recognition or to signal quality in conspecifics).

[Figure 1 about here.]

The distribution of circularly polarized patterns across the body of *G. falcatus* suggests its role in communication during conflict behaviour. The pattern is most prevalent on the tail, ventral and frontal side of the legs and head of

the animal, all regions which are preferentially exposed during confrontations with other mantis shrimps. In these aggressive interactions, the animal curls its abdomen underneath the body to present the heavily armoured tail as a shield [19, 20], with the result that the circularly polarized head, legs, and tail are most visible to the opponent (Figure 2). It is therefore possible that CP would elicit a fight-or-flight response in many different scenarios (e.g. territorial behaviour).

[Figure 2 about here.]

Behavioural discrimination of circular polarization

In a behavioural discrimination experiment, *G. falcatus* were trained, using a food reward, to grab either a left-hand circularly polarized (LCP) or right-hand circularly polarized (RCP) target. When tested subsequently using a two-alternative forced choice paradigm, these animals showed a clear preference for their trained circularly-polarized target over an alternative unpolarized target (85% preference; P=0.02; see Figure 3). However, when presented with an alternative target of the opposite-handed circular polarization to their trained target, *G. falcatus* showed no preference (45 out of 95 runs, P = 0.6, see Table S1). In these experiments, an initial training period involved presenting the animals with two targets, where the primed stimulus (i.e. LCP or RCP) had food attached to it and the other did not. During the testing phase, exactly the same regime was used as for training, except that in two of every three runs (each morning, noon, and afternoon) no food was present. To avoid olfaction bias, the test targets did not come in contact with food at any point. In the other of the three runs, food was present on the trained stimulus and served to reinforce the learned behaviour. The order in which the testing and training runs were delivered was randomised within each block of three presentations.

[Figure 3 about here.]

The ability to detect CP is conveyed by the proximal rhabdomal cell (R8) in rows 5 and 6 of the ommatidial midband, which functions as an achromatic

quarter-wave retarder [21]. This birefringent structure converts incoming light from circularly to linearly polarized, the outgoing axis of which depends on the handedness of the incoming light. The resulting linear polarization is then detected by the underlying linear polarization sensitive and spectrally broadband sensitive rhabdomers (R1-7). Similar forced choice food association experiments demonstrated that the peacock mantis shrimp (*O. scyllarus*) could be trained to discriminate between LCP and RCP [17]. Over recent years, at least four different mantis shrimp species have been shown to produce (via reflection or transmission) strongly circularly polarized body patterns on their cuticle (*O. cultrifer* [17], *G. falcatus*, *Neogonodactylus festae*, *N. austrinus*, and *N. oerstedi* (unpublished)). These differences in CP patterns and visual capabilities may depend on morphological and or behavioral differences that have evolved during these species' diversification – for example, *Odontodactylus* and *Gonodactylaceus* are relatively distantly related [22].

Circular polarization as a signal of burrow occupancy

Since *G. falcatus* both displays CP and can discriminate CP from UP it was important to determine if these marine crustaceans have any natural behaviour linked to this unusual light modality. After being displaced, many stomatopod species seek the safety of an empty hole or refuge, avoiding those that are already occupied by other mantis shrimps. Attempting to enter an occupied burrow can result in a damaging and potentially deadly confrontation [23]. Therefore, avoiding burrows that show signs of occupancy allows stomatopods to reduce the risk of injury. It has already been established that stomatopods use other cues, such as olfaction, to signal burrow occupancy [23]. It is possible that visual cues also contribute to this as part of a multi-modal signal. We therefore tested whether circular polarization affects refuge selection behaviour in *G. falcatus*.

Animals were presented with two burrows: one 'with' circular polarization and one 'without'. Three different experimental setups were used. 1) *Burrow entrance*- the animal was placed in a circular arena and provided with two burrows

to choose from (see Supplemental Movie "Burrow entrance.avi"). Each burrow entrance was partially blocked by, either an unpolarized filter, or a spectrally-similar circularly polarized filter. The filters resembled the stomatopod telson in shape (crescent) and size. 2) *Burrow end*- similar to (1) but the burrows were dimly backlit with unpolarized or circularly polarized light (see Figure 4 and Supplemental Movie "Burrow end.avi"). In this setup, the spectral differences between the two stimuli were minimal but some residual longwave LP light was reflected from the end of the burrow. 3) *Mono burrow end*- the arena had only one burrow which was backlit with either unpolarized or circularly polarized light. The light source used for the stimulus was split to illuminate the arena with spectrally identical ambient light and therefore eliminated any artefactual linearly polarized light (see Figure S1 in the Supplemental Information for a detailed spectrapolarimetry analysis of the stimuli used in this study).

In all three refuge experiments, the mantis shrimp avoided or delayed entering refuges giving off LCP light. When provided with a choice of burrows, most animals entered one within one minute. In the first experiment (*Burrow entrance*), the animals chose the burrow with an unpolarized (UP) crescent shape in the entrance in preference to an LCP crescent (58 out of 89 runs, 68% preference for UP, $P < 0.01$). Similarly, in the second experiment (*Burrow end*), animals preferred to enter burrows emitting UP light rather than burrows emitting LCP light (41 out of 48 runs, 88% preference for UP, $P < 0.001$). In the third experiment (*Mono burrow end*) stomatopods took 7 times longer to enter a single LCP backlit burrow than when the same burrow was backlit with UP light (48 ± 128 and 7 ± 8 (mean $\pm$ standard deviation) seconds for the LCP and UP respectively; 18 individuals each tested once for each of the two stimulus types during a period of two days; $P = 0.03$) (see Figure 3 and Table S1).

There are several reasons why circularly polarized body patterns may function as a cue for burrow occupancy. Firstly, elliptical polarization underwater is extremely rare. With the exception of reflective interactions within a few cm of the water's surface [24] and perhaps some birefringent structures in small pelagic

zooplankton [25, 26], elliptical polarization is largely absent from the underwater environment. For animals that can discriminate the circular polarization of light, any reflections of this kind will be highly salient against an unpolarized background. Secondly, polarized body patterns (indeed any polarization) have the advantage of being more reliable underwater than colour, which is affected by depth and illumination conditions [27, 28]. Certain wavelengths of light are rapidly attenuated with depth and this, combined with the shadowy ambient light environment of stomatopod refuges, would make colour a relatively unreliable signal. Polarization, however, would be relatively unaffected in this visual environment. Thirdly, we can make the relatively safe assumption that few, if any, species other than stomatopod crustaceans are able to discriminate the circular polarization of light. In this sense, these visual signals may function as covert communication patterns, simultaneously allowing the animal to be camouflaged in terms of colour and intensity (*G. falcatus* is coloured green or brown and is a good match to the reef substrate) while being clearly conspicuous in circular polarization.

The high avoidance rates recorded in this study suggest that circular polarization alone is a conspicuous cue, sufficient to elicit strong avoidance behaviour. An informative cue such as this may also form part of a signaling system for quick recognition by conspecifics at detection distances that may be far greater than olfaction detection distances. The signal's saliency, apparent rareness of the sensory mechanism needed to detect the signal, and the high cost associated with not detecting a conspecific or the detection of the stomatopod by prey or predator, all bolster our interpretation of the stomatopod's circular polarization as a covert signal.

Interestingly, other stomatopod species such as *Haptosquilla trispinosa* are known to use linear polarization signals for mate choice [29]. Such signals, while not visible to most reef fish as far as we know, would be clearly visible to the linear polarization vision of one of their major predators, the cephalopods. It is possible that CP signalling has evolved specifically to advance beyond the

detection by cuttlefish and octopus which, again as far as we know, lack circular polarization sensitivity.

This study provides the first evidence for the use of the circular polarization of light as a visual communication signal in any animal. While some scarab beetles were thought to use circular polarization [30], more thorough and recent experiments suggest this is unlikely [31]. We demonstrate that the mantis shrimp *G. falcatus* avoids refuges emitting circularly polarized light, preferring to occupy burrows emitting light of the same wavelength and intensity, but without the circular polarization component. Our interpretation for this natural response is that circular polarization may be used by this species as a private signal for burrow occupancy.

Experimental Procedures

In both the *Burrow end* and *Mono burrow end* setups the burrows were backlit through a reversible filter-bank (threaded 30 mm cage plate, 0.5" thick; Thorlabs, Newton, USA) with three filters in the following order: a) a circular polarizer (Edmund Optics, left-handed, 25mm diameter), b) a white diffuser (PTFE sheet; Dotmar EPP Pty Ltd, Acacia Ridge, Australia), and c) a 0.3 neutral density filter (Lee Filters, Andover, UK). The polarization visible to the stomatopod was dictated by the orientation of the filter-bank: while light travelling from the circular polarizer to the diffuser (and then to the neutral density filter) (a to c) was unpolarized, light travelling from (the neutral density filter to) the diffuser to the circular polarizer (c to a) was circularly polarized. Since the light passed through the same set of filters (albeit in reverse order) its transmitted intensity and spectrum (but not polarity) were identical irrespective of the orientation of the filter-bank. Differences in the spectrum or intensity of reflected light were minimised by the neutral density filter (c) in the filter bank (see Figure S1).

The choice arenas for the burrow experiments consisted of a gray PVC tube

(5.5 cm radius, 11 cm height) with a PVC bottom (Figure 4). White pebbles were distributed and glued evenly on the bottom to facilitate the animals' locomotion. Two holes (5 mm radius) placed 30° apart led to plastic tubes (4 cm long) which functioned as refuges. These positions were chosen to reflect the mean separation angle of the animal's eyestalks ($\sim 30°$; unpublished), ensuring that both refuges are easily visible from the centre of the arena (see Supplemental Information).

[Figure 4 about here.]

Statistical significance was tested using generalized linear mixed models. The results from the Discrimination, *Burrow entrance*, and *Burrow end* were binomial in nature, and so they were tested with a binomial error structure and a logit link function. Because the dependent variable in the *Mono burrow end* experiment was the amount of time it took the animals to enter the burrow, those were tested with a Gamma error structure and an inverse link function. All statistical analyses were performed in R (R version 3.0.2 and lme4 package)(see Supplemental Information).

Author Contributions

Conceptualization Ideas, Y.L.G., M.J.H., and N.J.M.; Methodology, Y.L.G.; Software, Y.L.G.; Formal Analysis, Y.L.G. and R.M.T.; Investigation, Y.L.G. and R.M.T.; Resources, Y.L.G., R.M.T., and N.J.M.; Writing Original Draft, Y.L.G. and M.J.H.; Writing Review & Editing, Y.L.G., M.J.H., R.M.T., and N.J.M.; Visualization, Y.L.G.; Supervision, M.J.H. and N.J.M.; Funding Acquisition, N.J.M.

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List of Figures

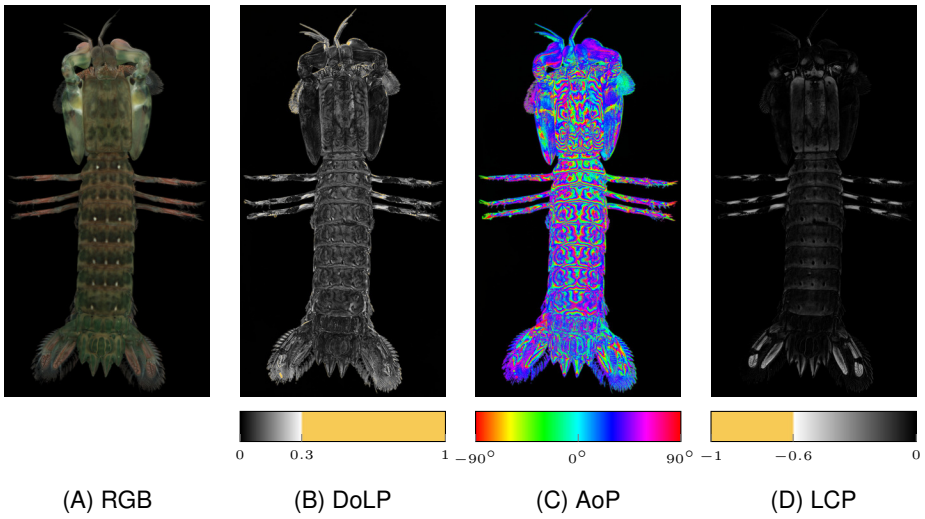

Figure 1: **Photopolarimetry of *Gonodactylaceus falcatus*:** (A) Gamma corrected and white balanced RGB representation of the animal. (B) Degree of Linear Polarization (DoLP); notice that since there were very few values larger than 0.3, the colour-bar was truncated at 0.3 (indicated by the yellow colour). (C) The Angle of Polarization (AoP). (D) The Degree of left-hand circular polarization (LCP). Since no right-hand circular polarization was reflected from the animal, an equivalent image for the right-hand circular polarization is not included. The colour-bar was truncated at an upper limit of -0.60. The photopolarimetry was obtained with a Nikon D300 fitted with two rotatable filter rings. One ring had a linear polarizing film while the other had a quarter-wave retarder film (American Polarizers, Reading, USA). By rotating these two rings (relative to each other and the camera's objective) the six required measurements for calculating the stokes vectors were obtained (horizontal, vertical, diagonal, anti-diagonal, right hand circular, and left-hand circular). In order to maintain the linear relationship between light intensity and pixel intensity, the images were saved in raw format (converting NEF files to TIFF was done with dcraw). All image processing was done in Julia [32] following previous photopolarimetry literature [33].

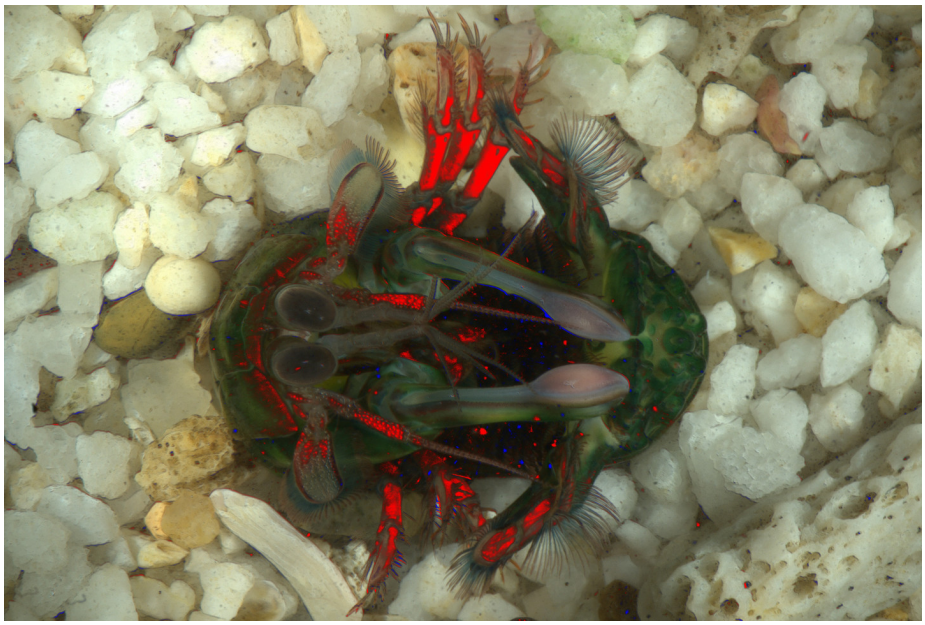

Figure 2: **Left-hand circular polarization in a defensive *Gonodactylaceus falcatus*:** The animal was manually positioned and placed to resemble its natural defensive posture. The red colour indicates degree of left-hand circular polarization reflected from the body of a *G. falcatus* in a typical defensive posture. Notice how the highly polarized uropods, legs, and head are visible for a potential viewer/attacker suggesting a connection between circular polarization signaling and aggression.

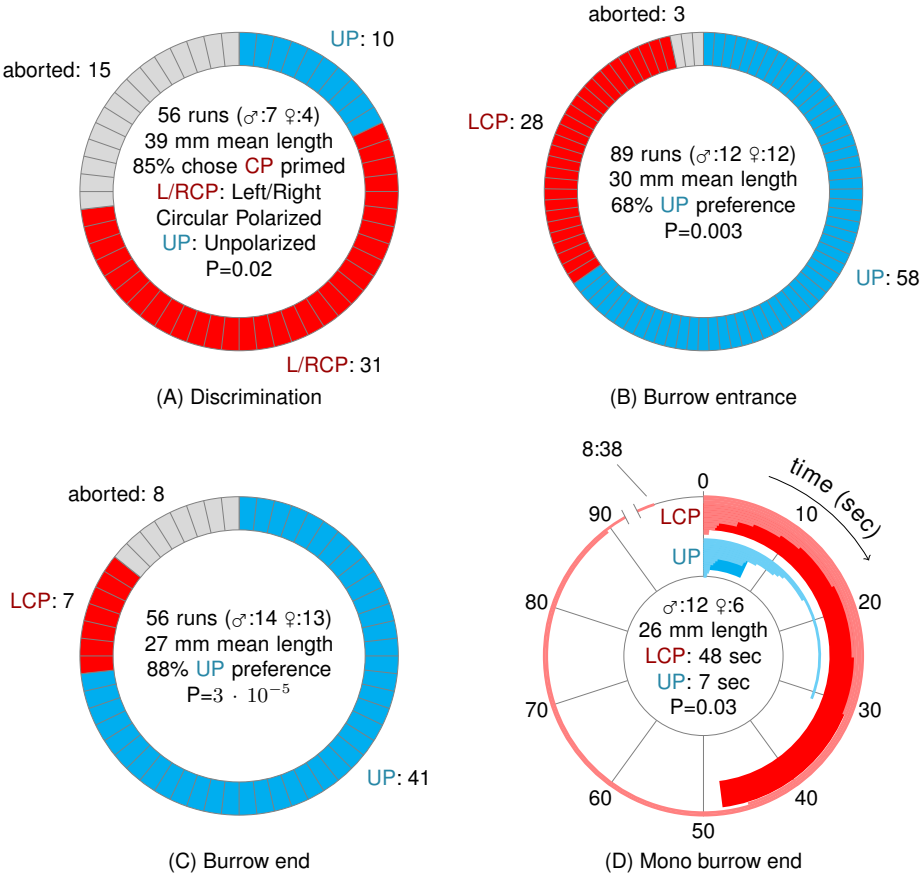

Figure 3: **Summary of the results for all experiments:** Each pane presents the results from one of the behavioral experiments in this study. In the center of each pane are the number of total runs, number of individual male and female *Gonodactylaceus falcatus*, mean body length, main result (i.e. choice, preference, or duration), and its respective P value. Unpolarized (UP) and left or right circularly polarized (L/RCP) stimuli are denoted by the blue and red colors respectively. (A) Behavioral discrimination: *G. falcatus* were successfully trained to discriminate between L/RCP and UP targets. Panes (B)–(C) summarize the results from the three natural preference experiments with *G. falcatus*. (B) *Burrow entrance*: Stomatopods naturally preferred burrows with a UP crescent-shaped filter at the burrow's entrance over burrows with an LCP filter. (C) *Burrow end*: The same preference was exhibited when the mantis shrimps were presented with a choice between dimly backlit burrows. (D) *Mono burrow end*: When the animals were presented with a single, dimly backlit burrow, they took about 7 times longer to enter the burrow when it was backlit with LCP than UP light. The ordered histograms show the distribution of the durations in seconds (note that one of the CP runs lasted for 8 minutes and 38 seconds). The group means are depicted by the thicker bars in the background.

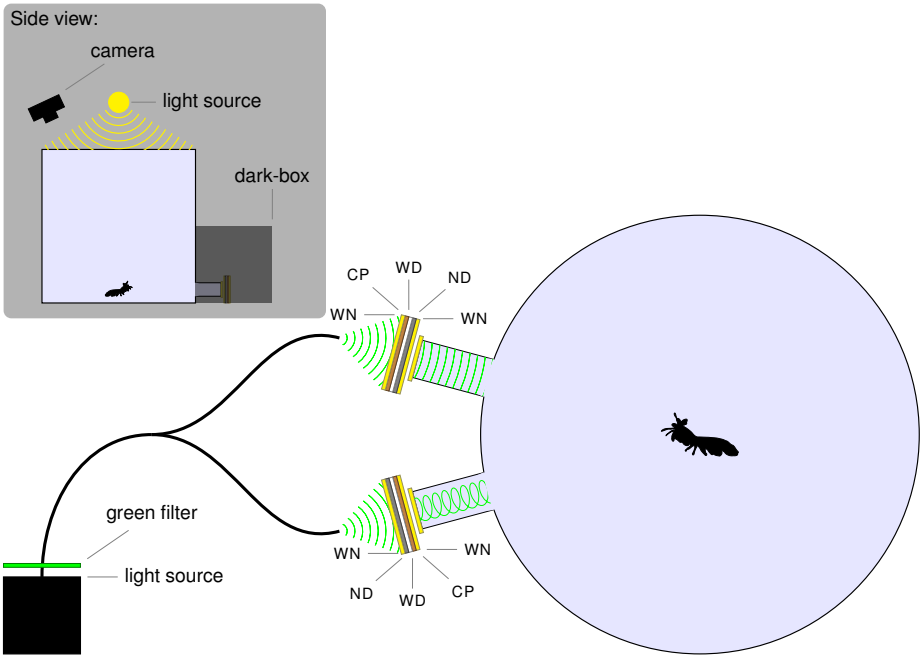

Figure 4: **The layout of the *Burrow end* setup for the natural preference experiments:** White light was filtered (interference filter with a λ_{max} of 500 nm), bifurcated, and aligned to shine down the burrows. The light travelled through a bank of filters before reaching the glass window at the end of the burrow. The bank of filters contained: glass window (WN), left-hand circular polarizer (LCP), white diffuser (WD), neutral density filter (WD), and another glass window (WN). In this order, the light passing through this filter-bank was unpolarized (see 'top' burrow). In the case where the filter stack is reversed, the light passing through was circularly polarized (see 'bottom' burrow). The stomatopod's behaviour was monitored from a small webcam.